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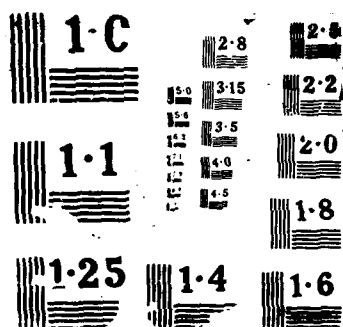
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19 ABSTRACT (Continue on reverse if necessary and identify by block number) We have digitized the cone centers of a primate and a human photoreceptor lattice and have determined that the Nyquist limit predicts visual resolution out to nearly two degrees of retinal eccentricity. Beyond 2 degrees lattice disorder appears to have a deleterious effect on resolution. Comparison of rod and cone capture areas shows compensatory factors between cone density and aperture size. A developing model of lattice structure and design strategies reflects complex principles involved in the evolution of human spatial vision. We are currently exploring a "bottom up" model of human vision where sampling limitations are propagated along the spatial vision processing hierarchy. The observations that this model addresses include a new class of two-dimensional spatial discriminations where we have discovered that the center of a circle can be discriminated more accurately than the bisection of two points of comparable separation. This discovery has lead to the development of two additional lines of research, area discrimination and dot density					
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20. Abstract (continuation)

discrimination. We have identified a fundamental similarity between spatial-frequency discrimination and vernier acuity that demonstrates that Weber's Law applied similarly to both tasks. Further, we have shown that two-dot vernier discrimination falls off within two degrees of retinal eccentricity similarly to changes in retinal sampling. These findings contribute to a model of spatial discriminations that includes limits imposed at the sampling level of the visual process.

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I. SUMMARY

The three specific aims of this project include: 1) the characterization of the human and monkey photoreceptor lattice; 2) the study of new spatial discriminations in two-dimensions including circle center, area, and dot density discriminations, and 3) the expansion and generalization of current models of one-dimensional spatial discriminations such as spatial-frequency, line separation, and vernier acuity.

We have digitized the cone centers of a primate and a human photoreceptor lattice and have determined that the Nyquist limit predicts visual resolution out to nearly two degrees of retinal eccentricity (Hirsch and Miller, 1987; Hirsch and Curcio, 1987). Lattice disorder appears to have a deleterious effect on resolution beyond two degrees (Hirsch and Miller, 1987). Comparison of rod and cone capture areas shows compensatory factors between cone density and aperture size (Samy and Hirsch, 1987).

We have developed a new class of two-dimensional spatial discriminations, and have discovered that the center of a circle can be discriminated more accurately than the bisection of two points of comparable separation (Hirsch and Groll, 1987). This discovery has led to the development of two additional lines of research, area discrimination and dot density discrimination.

We have identified a fundamental similarity between spatial-frequency discrimination and vernier acuity that demonstrates that Weber's Law applies similarly to both tasks (Hirsch and Groll, 1987). Further, we have shown that two-dot vernier discrimination falls off within two degrees of retinal eccentricity similarly to changes in retinal sampling (Groll and Hirsch, 1987). These findings contribute to a model of one-dimensional spatial discriminations that includes limits imposed at the sampling level of the visual process. We have recently expanded our approach to the study of one-dimensional spatial discriminations to include the question, "how long does it take for a spatial discrimination?" and have discovered that discrimination of high spatial-frequencies requires a shorter duration than low spatial-frequencies (Gallant and Hirsch, 1987). The over-all goal of these three research aims is a comprehensive model of retinal sampling and impact on spatial discriminations.

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II. SPECIFIC AIMS OF CURRENT RESEARCH:

Aim 1: Photoreceptor Sampling.

To determine the human and primate cone sampling array and relate characteristics of the lattice to limits of spatial discrimination.

This effort includes determination of the foveal cone positional uncertainties associated with the photoreceptor sampling array of both monkey and human lattices. Various local and global indices of lattice quality including autocorrelation functions, radial and angular comparisons with a perfect lattice, and simulation of the lattice will be developed. Properties of the lattice will be related to one and two-dimensional spatial discriminations.

Aim 2: Two-Dimensional spatial discriminations:

To study the accuracy with which observers can discriminate two-dimensional variables.

Our studies of 2-D spatial discrimination tasks introduce a new type of spatial discrimination that expands the present models of spatial vision from one to two dimensions. We introduce area as a spatial variable, and measure the accuracy to which observers can locate the center of two-dimensional stimuli such as circles.

Aim 3: One-Dimensional spatial discriminations:

To further develop and expand the scaled lattice model of spatial discrimination based on one-dimensional spatial tasks such as vernier, line separations, spatial-frequency discrimination and sampling properties of the foveal photoreceptor lattice.

This effort includes comparison of foveal vernier acuity and spatial-frequency performance, development of an interleaved paradigm to study the fine structure of spatial discrimination functions, application of a masking and temporal paradigm to study the influence of duration on one-dimensional spatial discrimination tasks, and measurement of two-dot vernier performance from the fovea out to approximately two degrees of retinal eccentricity to relate changes in the photoreceptor lattice structure to changes in vernier discrimination.

III. PROGRESS ON AIM 1: PHOTORECEPTOR SAMPLING

A. Primate Lattice: Does cone positional disorder limit resolution?

We have measured the spacings between all cones in a strip of primate retina extending from the foveal center to approximately 5.75 temporal horizontal degrees of retinal eccentricity and in a circular window with a diameter of 1.0 degree. The strip is partitioned into 25 contiguous square windows and the circle is partitioned into six wedges. Positions of the cone centers in each lattice window are digitized for analysis of lattice structure and quality, and used to compare lattice properties at different retinal eccentricities and meridia. We find a monotonic increase in cone spacing with retinal eccentricity and meridional symmetry within the central one degree. Further we demonstrate that estimates of center-to-center spacing vary with both window size and retinal location. Retinal sampling limits based on the sampling theorem and a correction for hexagonal packing are consistent with measures of human acuity along the same meridian from the foveal center to about 1.25 degrees of retinal eccentricity. Beyond about 1.25 degrees of retinal eccentricity these sampling boundaries overestimate human acuity. Lattice disorder, which is equivalent in its effect to increased receptor spacing, can account for the divergence of visual resolution and sampling limits from approximately 1.25 to 4.0 degrees of retinal eccentricity. Beyond 4.0 degrees of retinal eccentricity visual acuity may be additionally limited by other neural factors.

B. Human Lattice: Sampling by the Human Retina Predicts Grating Resolution Within 2.0 Degrees

Cone center-to-center spacings were determined on a strip of human retina extending from the foveal center along the temporal horizontal meridian to approximately 2.0 degrees of retinal eccentricity. The retina was obtained from a 35 year old male (H4 of Curcio *et al.*, 1987) and has a cone density close to the average reported for young adults. A retinal whole mount (Curcio *et al.*, 1987) was viewed with Nomarski differential interference microscopy at a level just vitreal to the ellipsoid-myoid junction. Positions of the cone centers were digitized from photomicrographs and the distributions of nearest-neighbor distances (Hirsch *et al.*, 1984, 1987) were obtained for adjacent 0.165 deg^2 windows. We find an increase in receptor spacing over this 2.0 degree region that is similar to that previously reported for monkey and human. Application of the sampling theorem to these average spacing data identifies the Nyquist frequency, the highest spatial-frequency that can be unambiguously reconstructed by the retinal mosaic. We find that Nyquist frequencies for these retinal windows predict conventional measures of visual resolution. Thus, within 2 degrees of the foveal center, resolution as measured by conventional techniques is limited primarily by receptor sampling.

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C. Rod and Cone Capture Areas for monkey and human retina

We have measured the photon capture areas associated with rod and cone photoreceptors at the ELM of both human and monkey retinal mosaics. Although cone density falls exponentially with eccentricity, i.e.

$$\text{cone density} = 53,184 \times x^{-0.66}$$

(where x is retinal eccentricity in degrees and density is specified in counts per mm^2), the retinal area subtended by the cone capture region falls approximately linearly with eccentricity. Cones occupy 100% of the capture area in the foveal region, and only approximately 75% of the area by about 6 degrees. Therefore, the fall-off in density is much faster than the fall-off in the capture area. This is due to the exponential increase in cone diameter with eccentricity:

$$\text{cone diameter } (\mu) = 4.7 \times x^{0.28}$$

(where x is retinal eccentricity in degrees), which compensates in part for the rapid reduction in density. Continuing efforts will focus on a model of the structural dynamics of the retina and predictions for limits of visual sensitivity.

IV. PROGRESS ON AIM 2: 2-D SPATIAL DISCRIMINATIONS

A. Center Offset Discrimination is Better for Circles than for Two Dots with Comparable Diameters and Separations

We have compared discrimination of horizontal offset from the geometric center of circles and two-dot bisection stimuli. Center offset discrimination was measured for circles ranging in diameter from about 0.34 to 2.0 degrees and compared to two-dot bisection performance with dot separations equal to the circle diameters. We find that for small stimuli (diameter ≤ 0.5 degrees), just-noticeable-differences, jnds, in circle center offset Δc and jnds in two-dot bisection Δb are approximately equal. For larger stimuli, performance on the two-dimensional circle task progressively exceeds performance on the one-dimensional bisection task. A similar advantage is achieved for center offset discrimination of an ellipse when the horizontal diameter is set at 1.0 degree and the vertical diameter varies. We find that when the vertical diameter is smaller than about 0.5 degrees, the jnd in center offset Δe is equivalent to Δb for the comparable bisect task. For larger ellipses, Δe equals Δc for the comparable circle. Further we demonstrate that a two-dimensional stimulus can be degraded to as few as 4 dots with no deleterious effect on the center offset jnd. These results suggest that the human visual system is apparently able to exploit a two-dimensional spatial parameter, perhaps area, in order to achieve a discrimination advantage.

B. Area Discrimination

Continuing in the direction of Aim 2 we are developing an experimental paradigm to determine the jnd in circle area. Overall, Weber's Law describes one-dimensional discriminations in spatial-frequency, line separation and vernier acuity. However, no relationship has been described for discrimination of area. These experiments will follow a similar discrimination paradigm as previously developed for one-dimensional discriminations (Hirsch and Hylton, 1982, 1984, 1985 and Groll and Hirsch, 1987), and will determine the $\Delta A/A$ for circles over a range of circle area, A.

C. Dot Density Discrimination

Discrimination of dot density, ΔD , provides a probe of human spatial information limits. We intend to determine $\Delta D/D$ over a range of reference densities, D, for various circle diameters and relate the discrimination function to the sampling limits of retina. These experiments will lead to a model of information efficiency based on sampling density.

V. PROGRESS ON AIM 3: 1-D SPATIAL DISCRIMINATIONS

A. A fundamental similarity between vernier-offset discrimination and spatial-frequency discrimination.

The jnd in vernier offset Δv falls off with decreasing two-dot separation s similarly to the jnd in spatial-frequency Δf with increasing reference frequency f . Overall vernier offset discrimination tends to be slightly lower (higher resolution) than spatial-frequency discrimination. The fractional resolution in two-dot vernier offset discrimination $\Delta v/s$ plotted against dot separation in deg^{-1} yields a function similar to fractional resolution in spatial-frequency $\Delta f/f$ plotted against reference f . We find that $\Delta v/s$ plotted against s is approximately constant for both tasks demonstrating that Weber's Law generally applies for both vernier offset discrimination and for spatial-frequency discrimination. These results suggest that resolution for both two-dot vernier offset and spatial-frequency discrimination may be mediated by common scaling mechanisms and constrain general models of spatial discrimination.

B. Two-dot vernier discrimination within 2.0 degrees of retinal fovea

We have studied two-dot vernier discrimination as a function of dot separation at five retinal eccentricities between and including the fovea (0.0 degrees) and 2.0 degrees. We find an increase in the just-noticeable-difference, jnd, in vernier offset with retinal eccentricity and also an increase in the smallest dot separation at which the vernier task could be performed under our experimental conditions. Further, we find that the vernier just-noticeable-difference rises faster with eccentricity than the center-to-center distance between the photoreceptors. Thus as eccentricity increases from 0.0 to 2.0 degrees, progressively fewer hyperacuity level vernier jnds are measured. These data confirm that the limits of spatial discrimination are compromised beyond a very restricted central region of the fovea.

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C. Masking reduces separation and spatial-frequency discrimination more at larger than smaller spacing

We investigated the influence of temporal factors on line-separation and spatial-frequency discrimination using backward masking. In our procedure, each trial involved the sequential presentation of reference, test, and mask patterns. A 500 msec reference pattern was followed by a 500 msec delay and then by a 20 msec test pattern. After a variable interval, a 500 msec masking grating appeared. Fractional jnds ($\Delta s/s$ or $\Delta f/f$) were determined for reference separations and frequencies corresponding to 1, 4, 8, 12, and 16 cycles per degree. Each separation and frequency was examined over a range of test-mask temporal separation intervals from 20 to 100 msec. For all separations and spatial-frequencies tested, the fractional jnd increased as the interval between test and mask patterns decreased. However, the fall off in the fractional jnd depended upon separation or spatial frequency. The larger the separation (or lower the spatial frequency), the greater the deleterious effect on fractional jnd with masking. These results suggest that spatial discriminations require temporal exposures which covary with the size of the stimulus.

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VI. PUBLICATIONS, MANUSCRIPTS, PRESENTATIONS AND THESES:

Aim 1: Photoreceptor sampling

Hirsch, J. and Miller, Wm. H. (1987) Does cone positional disorder limit near-foveal acuity? J. Opt. Soc. Am. A, 4(8) 1481-1492.

Hirsch, J. and Miller, W.H. (1987) The sampling theorem overestimates acuity beyond 1.25 degrees of eccentricity. Supplement to Investigative Ophthalmology and Visual Science, 28, p. 360.

Hirsch, J. and Curcio, C.A. (1987) Sampling by the human retina predicts grating resolution within 2.0 degrees. (Presented at OSA annual meeting, Rochester). Technical Digest, Optical Society of America, p. 83.

Hirsch, J. and Curcio, C.A. (1987) The Spatial information capacity of the human fovea. In preparation. (Nature).

Samy, C. and Hirsch, J. (1987). Comparison of human and monkey photoreceptor lattices suggests evolutionary adaptations associated with a larger eye. In preparation. (Vision Research).

Aim 2: 2-D Spatial discriminations

Hirsch, J. and Groll, S.L. (1986) Discrimination of the center position of a circle exceeds discrimination of the center position between two dots for stimuli beyond a critical size. Technical Digest, Optical Society of Am., p. 111.

Hirsch, J. and Groll, S.L. (1987) A two-dimensional surround provides a bisection advantage. In preparation. (Vision Research).

Aim 3: 1-D Spatial discriminations

Hirsch, J. and Groll, S.L. (1987) Comparison of vernier offset discrimination and spatial-frequency discrimination. Spatial Vision. (accepted with minor revisions).

Groll, S.L. and Hirsch, J. (1987) Two-dot vernier discrimination within 2.0 degrees of retinal fovea. J. Opt. Soc. Am. A, 4(8) 1535-1542.

Groll, S.L. and Hirsch, J. (1986) The Weber fraction for vernier discrimination ($\Delta v/s$) increases between the fovea and approximately 2 degrees of retinal eccentricity and levels off from 2 to 5 degrees. Supplement to Investigative Ophthalmology and Visual Science, 27, p. 341.

Gallant, J.L. and Hirsch, J. (1987) Masking reduces separation and spatial-frequency discrimination more at larger than smaller spacing. Supplement to Investigative Ophthalmology and Visual Science, 28, p. 360.

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4. Yale Medical Degree theses:

- Subba R. Gollamudi (1987) "An evaluation of corrected loss variance as a useful visual field index in Glaucoma".
- Eric R. Jankelovits (1987) "The assessment of retinal function in cataract patients using laser interferometry"
- Peggy M. Liao (1987) "Corrected loss variance can discriminate between glaucoma suspect patients with no loss of visual sensitivity and control observers"
- David Bruce Granet (1987) "Vernier acuity and motion: A comparison of athletes and non-athletes"

In progress:

- Lesli M. Sims "Computerized static perimetry: An assessment of visual field changes before and after focal photocoagulation for diabetic edema"
- Michael Morris "Pre and Post IOL implant measures of visual resolution using laser interferometry"
- Chander Samy "Rod and cone areas as a function of retinal eccentricity"

5. Yale Ph.D. Thesis (in progress)

- Jack Gallant "Temporal factors in spatial discrimination"

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VII. PROFESSIONAL PERSONNEL

<u>Name</u>	<u>Title</u>
1. Joy Hirsch, Ph.D.,	Associate Professor P.I.
2. Susan L. Groll, Ph.D.,	Research Associate
3. Janet Hescock,	Laboratory Assistant
4. Art Belanger,	Systems programmer

Students

1. Jack Gallant	Yale Ph.D. student (1989)
2. Subba Gollamudi	Yale Medical Student (received M.D. 1987)
3. Eric Jankelovits	Yale Medical Student (received M.D. 1987)
4. David Granet	Yale Medical Student (received M.D. 1987)
5. Peggy Liao	Yale Medical Student (1988)
6. Leslie Sims	Yale Medical Student (1989)
7. Michael Morris	Yale Medical Student (1990)
8. Chander Samy	Yale Medical Student (1991)

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